Effects of environmental factors on species richness patterns of herb layer in Eastern Zhongtiao Mountain

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Abstract: The species richness of herb layer was investigated among 43 plots of forest vegetation in the eastern Zhongtiao Mountain, in southern Shanxi Province, China. The forest vegetation was divided into two major vegetation types such as the deciduous forest and the coniferous forest by the two-way indicator species analysis (TWINSPAN). The species richness of herb layer was fitted in the topographic and soil feature factors, as well as the topographic relative moisture index (TRMI) by the generalized linear models (GLM). The results showed that canopy cover and altitude were the most significant environmental factors. Soil pH value and soil nutrients index such as total N, organic matter content had no significant influence. The effect of environment factors on species richness of herb layer had significant difference in vegetation types. For the broad-leaved forest, litter depth and TRMI were the important environment factors. For the coniferous forest, soil clay content was another important environment factor. The range of environmental gradient such as altitude may contribute to the difference.

Keywords: Eastern Zhongtiao Mountain; Altitude; Canopy cover; Broad-leaved and Coniferous forests; GLM; Soil nutrients

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Introduction

The study on the relationship between species richness and environmental factors is a central goal in ecology. Ground vegetation can be considered as an environmental indicator because of its response to disturbance and management practices (Dale *et al.* 2002). Herbaceous layer vegetation typically accounts for the largest component of deciduous forest and may provide important indications for site quality, overstory regeneration patterns, ecosystem integrity, and conservation status (Small *et al.* 2002). Patterns of species richness appear to be the result of environmental conditions at larger scales and the complex interactions among biological and physical variables at smaller scales (Brockway 1998). The influence of one environmental factor may be masked by other environmental factors at a certain studied scale. For the differences of habitat condition, plant ecological needs and tolerance range, the effects of environmental factors on understory species richness are distinguishable according to the plot conditions (Härdtle *et al.* 2003). Understanding the relationship between species richness of herb layer and environmental factors may lead us to take reasonable measures in management. Previous studies in the Eastern Zhongtiao Mountain showed that altitudinal gradient determined the patterns of species diversity (Zhang *et al.* 2002, 2003). However, the difference of species richness patterns between vegetation types was neglected in those studies. There were few studies on the effect of environmental factors on species richness of herb layer in Zhongtiao Mountain. The main objective of this paper is to find out the species richness patterns of herb layer and identifying the environmental factors in the Eastern Zhongtiao Mountain.

Methods

Study area

The study was conducted at the eastern Zhongtiao Mountain (34°36′–35°53′N, 110°15′–112°37′E) with topography characteristics of steep hillsides and flat peaks, which was located in southern Shanxi Province, China (Fig. 1).

The elevation ranges from 500 to 2320 m a.s.l. The climate of this area shows a warm-temperate continental monsoon feature, which has distinctive four seasons with the most rainfalls pouring down in the hot summer. The mean annual temperature is 11°C and the mean annual precipitation ranges from 500–580 mm in the west to 600–720 mm in the east (Dendrologia Zhongtiaoshanensis editorial committee 1995). The vertical spectrum of vegetation zones from piedmont to the top in Zhongtiao Mountain is *Pinus-Quercus* forest zone (800–1 500 m), *Quercus variabilis* forest zone (1400–2000 m), *Populus-Betula* forest zone (1 900–2 200 m) and mountain meadow zone (2 100–2 320 m), (Zhang *et al.* 1997). Lishan Nature Reserve was established in the Eastern Zhongtiao Mountain to preserve the warm temperate forest and animal species in 1983, which was the largest national nature reserve with the richest biodiversity in Shanxi Province.

Sampling

In July 2003, 43 plots (Fig. 1) were sampled at an elevation interval of 50 m. Each sample plot was a square of 400 m^2 and was divided into four 100-m^2 subplots (Fig. 2). Percent of canopy cover and diameter at breast height (d.b.h) for all trees (> 5m high) were recorded according to the species in a pair of oblique opposite subplots of each plot. In the other two subplots, only tree composition was recorded for calculating relative frequency

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of the tree species in the whole 4 subplots. A herb quadrat of 1m×1m was randomly placed in each of the subplots. Then in each herb quadrat, the floristic composition of herbaceous species was recorded. The location of each plot was determined with a handy instrument of global positioning system (GPS, eTrex Vista model, made by Garmin in Taiwan in 2003) and then marked on a 1:50 000 map. Soil samples at 20-cm depth were taken at the center of the two subplots within each plot. The soil depth was determined by probing a 1-m-long graduated steel rod into the ground till it reached the bedrock. Evidence of disturbance was recorded for each plot and other factors that could influence the species richness such as altitude, slope, aspect and litter depth were also investigated. Soil samples were set air-dried and filtrated with a 2-mm sieve. The value of soil texture, soil pH value, total nitrogen and total organic matter were measured by standard procedures (Li 1983). Topographic Relative Moisture Index (TRMI), a measure of potential soil moisture based on topography that ranges from 0 (xeric) to 60 (mesic), (Parker 1982), was calculated with a Digital Elevation Model (DEM) of study area.

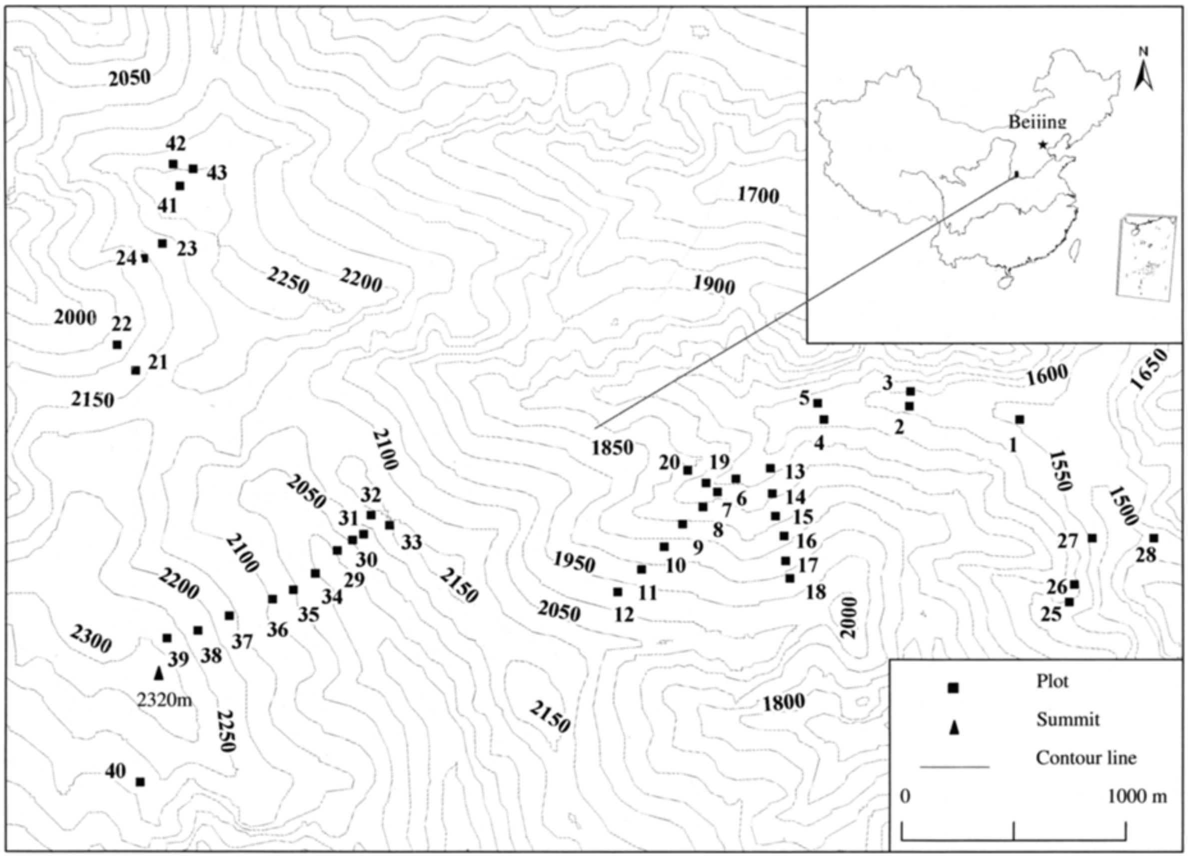

Fig. 1 Sketch map of study area, showing the location of Zhong Mountain in China. The investgated plots are marke. Countour interval is 50 m.

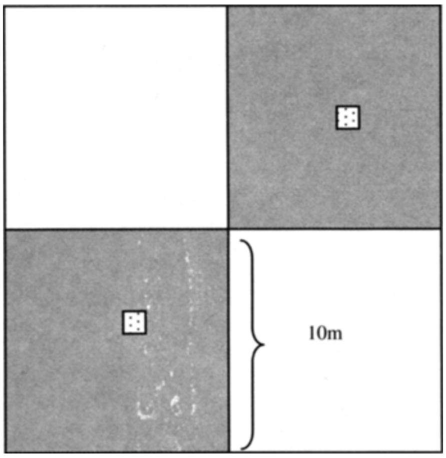

Fig. 2 The design of subplots and herb quadrats within a 400-m^2 plot. In the two hatched subplots of 100 m^2, community features were investigated in detail, and in the other two white subplots of 100 m^2, only tree compositions were recorded for calculating relative frequency of the species in the plot. The two spotted quadrats of 1 m^2 were herb quadrats randomly distributing in the 100-m^2 subplots respectively.

Data analysis

Species richness of herbaceous composition was determined as the total number of herbaceous species existed in the two herb quadrats within a plot. Major vegetation types were delimited by two-way indicator species analysis using TWINSPAN (Hill 1979). First, the importance value (IV) of tree species was calculated as the sum of relative breast height area, relative frequency and relative abundance, then, a TWINSPAN classification on the basis of the tree IV of the 43 plots was performed. The forest vegetation was classified into two types: deciduous forest and coniferous forest (Table 1).

The species richness was fitted with Generalized Linear Models (GLM) (McCullagh *et al.* 1989) for exploring a function of environmental factors. The total plots and the two major vegetation types were fitted by separate models. As the response variable consists of discrete data (counts), a Poisson error distribution was assumed and a logarithmic link function was used (Pausas 1994). For making the results more reliable, the collin-

earity of the employed factors was tested with Pearson correlation coefficients. Only one factor was used from pairs of inter-correlated factors (r>0.7, P=0.01).

Table 1. TWINSPAN result with the IV of 46 tree species in 43 plots

Species	Plots No.																																											Result of species				
	1	26	3	5	25	27	2	28	22	4	6	18	20	7	8	9	10	13	14	16	19	11	12	15	17	36	34	35	37	38	42	40	41	43	31	33	29	23	30	32	39	24	21					
Swida hemsleyi	-	-	-	-	-	-	-	-	2	2	-	2	-	-	1	-	-	-	-	-	-	-	1	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	
Ostrya japonica	-	-	-	-	-	-	-	-	-	-	3	-	-	2	-	-	-	2	3	1	2	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	
Betula platyphylla	-	-	-	-	-	-	-	1	-	-	2	-	-	2	1	3	3	-	-	3	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	1	0
Hydrangea bretschneideri	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	1	0
Crataegus sanguinea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	1	0
Cerasus clarofolia	-	-	-	-	-	-	-	-	2	-	-	-	-	2	1	1	-	-	-	1	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	1	0
Prunus padus	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	1	1
Acer grosseri	-	2	-	-	-	-	1	-	1	3	3	-	2	1	3	2	2	2	3	2	3	1	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	1	1
Cercidiphyllum japonicum	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	1	1
Ulmus laciniata	-	-	-	-	-	-	-	-	-	-	-	1	2	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	1	1
Prunus serrulata	-	-	-	-	-	-	-	-	-	2	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	1	1
Tilia paucicostata	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	1	1
Euonymus sanguineus	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	2	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	1	1
Rhamnus davurica	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	1	1
Philadelphus dasycalyx	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	1	0	
Syringa pubescens	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	1	0	
Carpinus cordata	-	-	-	-	-	3	3	2	-	2	3	3	2	2	2	2	2	3	1	3	2	3	3	1	3	3	5	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	1	0	
Acer truncatum	-	2	-	-	-	-	2	-	2	2	2	2	2	1	2	1	1	1	-	1	2	1	1	1	-	2	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	1	0	
Populus davidiana	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	2	1	-	3	3	3	3	4	1	-	3	-	-	-	-	-	-	1	-	-	-	-	-	-	-	0	0	1	1	
Fraxinus chinensis	-	3	-	-	-	1	2	-	-	2	2	-	1	1	1	-	-	1	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1			
Syringa pekinensis	1	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1			
Toxicodendron vernicifluum	3	-	-	-	-	-	3	2	-	2	-	1	1	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1			
Rhus potaninii	-	-	2	-	-	-	-	-	-	2	-	-	-	2	1	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1			
Viburnum sargentii	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0	
Juglans cathayensis	3	-	2	-	2	1	2	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0	
Ulmus davidiana	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	1	0
Quercus aliena	-	3	3	3	4	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	1	0
Crataegus maximowiczii	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	1	0
Quercus variabilis	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	1	0
Staphylea holocarpa	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	1	1
Carpinus turczaninowii	2	3	4	3	2	4	3	-	-	-	1	-	1	3	1	1	2	2	2	-	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	1	0	1		
Malus baccata	2	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	1	-	-	-	1	1	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	0	1		
Quercus liaotungensis	-	-	-	4	-	2	-	-	-	-	-	-	-	2	3	3	2	2	2	2	2	2	1	2	2	2	-	-	-	-	-	1	-	-	3	2	2	-	-	-	-	-	-	1	1			
Crataegus pinnatifida	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	1			
Sorbus discolor	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	2	-	-	-	-	1	3	1	2	-	-	2	-	2	2	-	2	-	2	1	-	-	-	-	-	-	-	0	0			
Salix tangii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	0	0			
Sorbus alnifolia	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	1	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	3	3	-	-	-	-	-	-	-	0	1	0		
Betula albo sinensis	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	2	1	-	1	-	-	-	-	-	-	3	3	3	-	3	-	-	-	-	-	-	3	0	1	1	0	
Picea wilsonii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	4	4	-	-	-	-	-	-	-	-	-	0	1	1	0	
Pinus tabulaeformis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	0	1	1	0	
Betula utilis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	5	-	2	2	-	-	1	-	-	-	-	-	-	0	1	1	1	
Salix caprea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	4	3	-	4	-	2	3	3	2	-	-	-	-	-	-	0	1	1	1	
Sorbus koehneana	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	1	1	
Larix principi rupprechtii	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	5	1				
Pinus armandi	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-	-	-	2	2	1	-	-	-	-	-	-	2	3	1	3	2	4	5	5	5	5	5	-	1				
Salix waliichiana	2	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1				
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1					
Result of plots division	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1					
	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1	1	1	0	0	0	0	0	0	1					

The factors were put into the model by a forward procedure (Pausas 1994; Vetaas 1997). Because the relationships between species richness and environmental factors are often curvilinear (Pausas *et al.* 2001), the simple polynomial function of each environmental factor is also tested. The goodness of model was measured with the change in deviance after including a variable in the model and was tested with an F-ratio test (McCullagh *et al.* 1989) at the confidence level of 0.05. The azimuth angle of plot topography is transformed to a radiation index (TRASP) (Roberts *et al.* 1989):

$$T_{RASP} = \frac{1 - \cos((\pi / 180)(aspect - 30))}{2} \quad (1)$$

Results

Vegetation classification

The forest vegetation was classified into two types by TWINSPAN classification (Table 1). One type is the deciduous forest, which was dominated by *Betula platyphylla*, *Acer grosseri*, *Carpinus cordata*, *Acer truncatum* and *Quercus liaotungensis*. The other type is coniferous forest, which was dominated by *Picea wilsonii*, *Larix principi-rupprechtii*, *Pinus armandi*, *Betula albo-sinensis* and *B. utilis*. The coniferous forest normally distributed much higher than the deciduous forest at altitude and the soil depth of the former was much deeper than that of the latter (Table 2). The canopy cover of two vegetation types had no distinct difference. The mean value of species richness in the coniferous forests was a little higher than that in the deciduous forests (Table 2).

Relationship between Species richness and environmental factors

After the test of collinearity, some environmental factors were excluded, which were soil organic matter content and sand content for the total plots (Table 3) and the deciduous forest, and for the coniferous forest, were TRASP, soil depth, soil pH value, soil organic matter and soil sand content.

In the total plots, the most significant environmental factors influencing the species richness of herb layer were canopy cover and altitude, followed by soil depth (Table 4). The three factors accounted for 47.6% of the deviance in species richness. Species richness showed a negative correlation with canopy cover, and a negative humped (relationship with altitude and soil depth (Fig. 3).

Table 2. The species richness of two vegetation types and the environmental factors of the total plots

Vegetation type		Richness	Altitude (m)	Slope degree(°)	TRASP	Litter depth (cm)	Soil depth (cm)	Canopy (%)	Soil pH value	Total N ($g \cdot kg^{-1}$)	Organic matter ($g \cdot kg^{-1}$)	TRMI	Sand (%)	Silt (%)	Clay (%)
Total plots	Min	5	1430	8	0	1	5	54	5.13	1.68	46	11	0.02	0.45	0.18
	Max	32	2280	40	1	10	48	94	6.85	9.09	274	46	0.33	0.76	0.35
	Mean	13.07	1897	25	0.35	3.75	19.54	78	6.14	4.17	122	30	0.1	0.65	0.25
Deciduous forest	Min	6	1430	10	0	1	5	54	5.13	1.68	46	11	0.02	0.45	0.18
	Maxi	32	2170	40	0.93	10	30	94	6.85	9.09	274	44	0.33	0.76	0.35
	Mean	12.24	1765	25	0.23	3.46	16.91	78	6.16	4.33	127	31	0.1	0.65	0.25
Coniferous forest	Min	5	2000	8	0.03	1	10	60	5.63	2	51	11	0.02	0.6	0.18
	Max	27	2280	30	1	8	48	93	6.68	7.04	251	46	0.16	0.69	0.3
	Mean	14.79	2169	24	0.59	4.36	24.96	78	6.08	3.85	110	27	0.08	0.66	0.26

Table 3. Pearson correlation coefficients between different environmental factors and the species richness of the herb layer for total plots (* = $P < 0.05$, ** = $P < 0.01$, n = 43)

Environmental factors	Altitude	Slope	TRASP	Litter depth	Soil depth	Canopy	Soil pH value	Total N	Organic matter	TRMI	Sand	Silt	Clay
Altitude	1	-0.35*	0.07	0.22	0.56**	-0.07	-0.15	0.14	0.12	-0.06	-0.27	0.24	0.12
Slope		1	0.17	0.1	-0.49**	-0.2	0.19	-0.31*	-0.23	0.03	0.17	0.07	-0.35*
TRASP			1	0.16	-0.07	0.03	0.06	-0.27	-0.33*	-0.42**	0.32*	-0.33*	-0.09
Litter depth				1	-0.08	0.14	-0.08	0.16	0.14	-0.16	-0.25	0.25	0.09
Soil depth					1	-0.13	-0.23	0.04	-0.02	-0.03	-0.22	0.17	0.13
Canopy						1	0.11	0.08	0.04	-0.2	-0.12	-0.19	0.42**
Soil pH valu							1	-0.05	0.03	-0.01	0.08	-0.32*	0.27
Total N								1	0.91**	-0.05	-0.1	-0.13	0.32*
Organic matter									1	-0.03	-0.07	-0.09	0.22
TRMI										1	-0.11	0.21	-0.08
Sand											1	-0.77**	-0.61**
Silt												1	-0.04

For the deciduous forest, the important environmental factors were canopy cover, litter depth, TRMI, and altitude, which accounted for 79.4% of the deviance in species richness (Table 4). Canopy cover was the most significant environmental factor and accounted for 40.2% of the deviance in species richness (Table 4). Species richness decreased with increasing canopy cover and litter depth, and increased with increasing TRMI (Fig. 3). And species richness had a negative humped quadratic response with altitude (Fig. 3). For the coniferous forest, altitude, soil clay content and canopy cover were the best predictors of species richness of herb layer, and 88.4% of the species richness's deviance was explained (Table 4). The relationships between species

richness and slope, TRASP, soil pH value, soil nutrients (total N, organic matter content) were not significant.

Table 4. GLM models for all plots and for the two vegetation types (* = *P* < 0.05, ** = *P* < 0.01)

	Model	Residual Deviance	*df*	Deviance explained (%)	F	*P*
All plots	Null	116.15	42			
	Canopy	83.03	41	28.5	17.92	**
	+ Poly(Altitude, 2)	70.12	39	39.6	3.49	*
	+ Poly(Soil depth, 2)	60.83	37	47.6	2.85	*
Broad-leaved forest	Null	77.96	28			
	Canopy	46.61	27	40.2	40.34	**
	+ Poly(Litter depth, 2)	33.13	25	57.5	8.67	**
	+ Poly(TRMI, 2)	20.47	23	73.7	8.15	**
	+ Poly(Altitude, 2)	16.06	21	79.4	2.84	*
Coniferous forest	Null	33.61	13			
	Poly (Altitude, 2)	20.46	11	39.1	13.9	**
	+ Clay	12.24	10	63.6	17.4	**
	+ Poly (Canopy, 2)	3.90	8	88.40	8.8	**

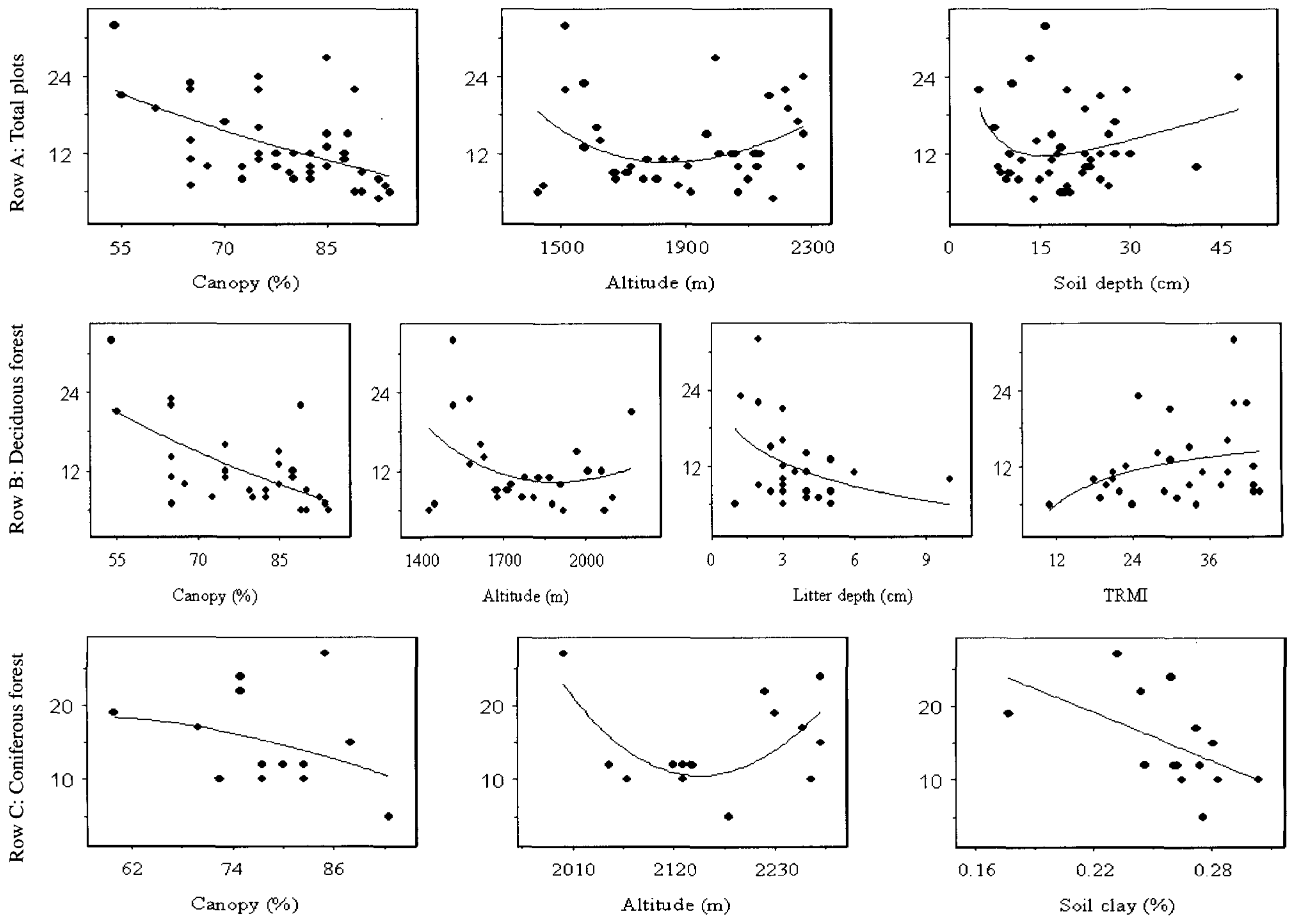

Fig. 3 Scatter plots of species richness with selected environmental factors for total plots (Row A),deciduous forest (Row B), and coniferous forest (Row C)

Discussion

In general, canopy cover was the most significant environmental factor influencing the species richness of herb layer, and high canopy cover would lead to low species richness. This kind of relationship was held in other studies (Tilman 1993; Brosofske *et al.* 2001; Härdtle *et al.* 2003; Qian *et al.* 2003). The underlying mechanism of this relationship may be that the shade-intolerant species were excluded by the reduction of light.

Altitude is also important environmental factor for species richness of herb layer, and in this study a humped curve between altitude and the species richness was held for the all plots and the two vegetation types. Similar pattern was found in the study of Qinling Mountains (Tang *et al.* 2004). As environmental heterogeneity tends to increase coexistence and maintain high richness,

the higher habitat heterogeneity at the ecotone of vegetation types may contribute to this pattern (Pausas *et al.* 2001).

For the two vegetation types, the canopy cover and altitude are still significant environmental factor, but the soil depth is no longer important environmental factor. Instead, ground litter depth and the soil clay content became the important environmental factors influencing the species richness of herb layer in the two vegetation types respectively. TRMI was important only for broad-leaved forest (Table 4). The scale of the environmental gradient might contribute to these changes. For deciduous forest, thicker litter layer led to lower species richness. It was explained that thick litter layer may inhibit seed germinating or increase mortality of seedlings and other small plants (Tilman 1993). A positive relationship between the soil moisture availability and species richness has been found in many studies (Pausas 1994; Härdtle *et al.* 2003; Kolb *et al.* 2004). In Pyrenean *Pinus sylvestris* forest, high radiation reduced the water availability to plants and led to low species richness (Pausas 1994). In moist forests, species richness has a close positive correlation with soil moisture (Härdtle *et al.* 2003). The same pattern has been found in the broad-leaved forest in our study.

Surprisingly, species richness in coniferous forest decreased with rising soil clay content. The fact that soil clay content is closely related with canopy cover, which has a strong negative influence to the species richness of herb layers, may also account for this phenomenon. Soil pH value and soil nutrients were not significant environmental factor for species richness in herb layer. It may be explained that their influences were masked by other environmental factors such as canopy cover and altitude.

The results consisted with the finding that the environmental factors have different effects on the species richness of the ground vegetation according to vegetation types (Härdtle *et al.* 2003). In our study, the explanatory power of environmental factors for the species richness of herb layer was improved significantly when the plots were separated and analyzed in different vegetation types, which consisted with the results of a study of forest in northern Wisconsin (Brosofske *et al.* 2001). The range of environmental gradient might contribute to this improvement. It is well known that vegetation types are good environmental indicators in analyzing the species richness of herb layer according to the overstory characteristics.

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References

Brockway, D.G. 1998. Forest plant diversity at local and landscape scales in the Cascade Mountains of southwestern Washington [J]. Forest Ecology and Management, **109**(3): 323–341

Brosofske, K.D., Chen, J. & Crow, T.R. 2001. Understory vegetation and site factors: implications for a managed Wisconsin landscape [J]. Forest Eecology and Management, **146**(1): 75–87.

Dale, V.H., Beyeler, S.C. & Jackson, B. 2002. Understory vegetation indicators of anthropogenic disturbance in longleaf pine forests at Fort Benning, Georgia, USA [J]. Ecological Indicators, **1**(3): 155–170.

Dendrologia Zhongtiaoshanensis editorial committee. 1995. Dendrologia Zhongtiaoshanensis [M]. Beijing: China Forestry Publishing House, p1-5. (in Chinese)

Härdtle, W., Oheimb, G.V. & Westphal, C.H. 2003. The effects of light and soil conditions on the species richness of the ground vegetation of deciduous forests in northern Germany (Schleswig-Holstein) [J]. Forest Ecology and Management, **182**(4): 327–338.

Hill, M.O. 1979. TWINSPAN: A FORTRAN Program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes [M]. New York: Cornell University, p90.

Kolb, A. & Diekmann, M. 2004. Effects of environment, habitat configuration and forest continuity on the distribution of forest plant species [J]. Journal of Vegetation Science, **15**(2): 199–208.

Li Youkai. 1983. Normal Analysis Methods of Soil and Agrichemistry [M]. Beijing: Science Press, p281–291. (in Chinese)

McCullagh, P. & Nelder J.A. 1989. Generalized Linear Models. 2nd ed [M]. London: Chapman & Hall.

Parker, A.J. 1982. The topographic relative moisture index: An approach to soil-moisture assessment in mountain terrain [J]. Physical Geography, **3**(2): 160–168.

Pausas, J.G. & Austin, M.P. 2001. Patterns of plant species richness in relation to different environments: An appraisal [J]. Journal of Vegetation Science, **12**(2): 153–166.

Pausas, J.G. 1994. Species richness patterns in the understorey of Pyrenean *Pinus sylvestris* forest [J]. Journal of Vegetation Science, **5**: 517–524.

Qian, H., Klinka, K., Økland, R.H. Krestov, P & Kayahara, G.J. 2003. Understorey vegetation in boreal *Picea mariana* and *Populus tremuloides* stands in British Columbia [J]. Journal of Vegetation Science, **14**: 173–184.

Roberts, D.W. & Cooper, S.V. 1989. Concepts and techniques of vegetation mapping [C]. In: Land Classifications Based on Vegetation: Applications for Resource Management. USDA Forest Service General Technical Report INT-257, Ogden, UT, pp. 90–96

Small, C.J. & McCarthy, B.C. 2002. Spatial and temporal variability of herbaceous vegetation in an eastern deciduous forest [J]. Plant Ecology, **164** (1): 37–48.

StatSci. 2000. SPLUS Guide to Statistical and Mathematical Analysis. MathSoft Inc., Seattle, WA.

Tang Zhirao & Ke Jinhu. 2004. Altitudinal patterns of plant species diversity in Mt. Niubeiliang, Qinling Mountains [J]. Biodiversity Science, **12**(1): 108–114 (in Chinese with English abstract)

Tilman, D. 1993. Species richness of experimental productivity gradients: How important is colonization limitation? [J] Ecology, **74**(8): 2179–2191.

Vetaas, O.R. 1997. The effect of canopy disturbance on species richness in a central Himalayan oak forest [J]. Plant Ecology, **132** (1): 29–38.

Zhang Feng, Zhang Jintun, Shangguan Tieliang. 2002. Plant diversity of forest community in Zhuweigou of Lishan Mountain Nature Reserve [J]. Acta Phytoecologica Sinica, **26**(supplement): 46–51. (in Chinese with English abstract)

Zhang Feng, Zhang Jintun, Zhang Feng. 2003. Pattern of forest vegetation and its environmental interpretation in Zhuweigou, Lishan Mountain Nature Reserve [J]. Ecologica Sinica, **23**(3): 421–427.

Zhang Jintun, Zhang Feng, Shangguan Tieliang. 1997. Reanalysis of vertical zones of vegetation in Zhongtiao mountain [J]. Journal of Shanxi University (Nat. Sci. Ed.), **20**(1): 76–79. (in Chinese with English abstract)